Towards more predictive and interdisciplinary climate change ecosystem experiments

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Improving the predictive power and interdisciplinarity of climate change experiments

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Preface (100 words)

While the general *direction* of ecosystems' responses to a variety of climate change scenarios has been well investigated, insights in the potential *amplitude* and *dynamics* of this response are scarce and the societal impacts often remain unquantified. Drawing on the expertise of researchers from a variety of disciplines, this paper outlines how methodological and technological advancements can help design climate experiments that better capture the dynamics and amplitude of ecosystem responses provoked by climate change and translate these responses into societal impacts.

1. Introduction

Climate change is expected to impact ecosystem communities and ecosystem functioning[1]. Crop yields[2], carbon (C) sequestration in soil[3], and pollination rate[4] are generally predicted to decrease, while land evapotranspiration[5] and tree mortality, especially in the Boreal region, are expected to increase[6]. At the same time, the redistribution of species will increase opportunities for pest and pathogen emergence[1].

These functions are crucial for human well-being through their contribution to ecosystem services, and so impacting them will have important consequences for society[7]. However, refining the societal cost estimations remains a challenge, partly because large knowledge gaps regarding the amplitude and dynamics of these responses that make it difficult to plan for climate adaptation. Specifically designed climate change experiments are necessary to address these issues. The goal of this perspective paper is fourfold. First, while acknowledging the great advances achieved by climate change-ecosystem responses experiments so far, we also identify the challenges that many of them currently face: high complexity of climate change in terms of environmental variables, constraints in the number and amplitude of climate treatment levels, and the limited scope with regard to responses and interactions covered (Section 2). Second, to overcome these challenges we propose an experimental design that can leverage the increased computational and technological capabilities to more accurately capture the complexity of climate change in experiments; increase the number and range of climate treatment levels, and employ an interdisciplinary approach to broaden the range of responses and interactions covered (Section 3). Third, we outline an experiment that applies these design recommendations to demonstrate how it can enhance our capacity to understand and predict ecosystem responses to climate change. We describe the technical infrastructure used in this experiment, the climate manipulations, and the analysis pathway all the way to the valuation of the changes in ecosystem services (Section 4). Fourth, we place this design within the larger context of climate change experiments and pinpoint its complementarity to other designs (Section 5).

2. Challenges of climate change experiments

The complexity of climate change

The first challenge for research on climate change-ecosystem responses lies in the complex manner in which global climate change will affect local weather. To mimic a future climate, factors such as air temperature, atmospheric CO_2, and precipitation need to be manipulated in combination, which can be both conceptually and technologically challenging[8]. Therefore, a significant proportion of climate change experiments have focused on measuring the effects of specific combinations of climate factors (such as warming plus drought), manipulated using technology that was available or affordable at that time (such as passive night-time warming and rain exclusion curtains)[9]. Although these experiments have led to many invaluable outcomes, such approaches cannot fully cover the complexity of climate projections or the covariance of meteorological variables. As such, they may, for example, under- or overestimate the effects on ecosystem functioning of changes in the frequencies of frosts and heat waves, drought-heat-wave reinforcements[10], interactions between soil moisture conditions and subsequent precipitation occurrence[11], increased frequencies of mild droughts (including in spring and autumn), and increased frequency of heavy precipitation events[12].

These climate alterations can have a strong influence on ecosystem functioning: for example, decreased frost frequency may have a significant impact on plant mortality[13] and more frequent mild droughts can trigger plant acclimation and hence resistance to drought stress[14]. Therefore, many climate change experiments did not simulate (i) an extreme event instead of a change in the mean for a given single factor, (ii) regimes of events instead of a single event for a given single factor, and (iii) complex coupling between multiple factors. This lack of refinement in climate manipulations likely compromised the reliability of the estimation of ecosystem responses. Some steps have already been taken to address this, by applying treatments of precipitation regime or heatwaves as observed in the field[15,16] and by using translocation experiments, where macrocosms are displaced across geographic gradients in order to expose them to other climates that match possible future conditions at the location of origin (space for time approach)[17]. However, such an issue cannot be solved by modelling alone, because it requires testing too many possible interactions between factors, as well as changing regimes of single factors.

Climate treatment levels: number and range

Because of the cost of specialized infrastructure, scientists are often limited in the number of experimental units they can set up within a given experiment. Hence, climate factors are often applied at only two levels: ambient and future projections[9]. This provides useful estimations on the direction of ecosystem responses but does not provide insights into the shape of the responses to these factors or how far away current conditions are from potential tipping points to alternative stable states[18]. Moreover, ecosystem responses to multifactor global change drivers are regulated by complex, nonlinear processes[19], which makes modeling difficult with experimental data that comes only from the two-level manipulation of environmental factors[20].

Also stemming from high equipment costs is the narrow range of climate treatments. Most experiments have kept this range within conservative boundaries[21], presumably because more drastic (though realistic) climate treatments may have a catastrophic impact on a studied ecosystem, potentially leading to the loss of expensively equipped replicates. The truncation of more extreme climate conditions has, in turn, led to a lack of evidence regarding their effects on ecosystem functioning.

Finally, low temporal resolution is also an issue. Because it requires an extensive and high frequency monitoring of ecosystem functions, a substantial proportion of climate change experiments have only measured the ecosystem dynamics or trajectories annually or seasonally. Such experiments may fail to detect short-term dynamics of ecosystem responses[22] or trajectories leading to a transition to an alternative stable state[23,24]. However, trends related to ecosystem dynamics often appear on decadal time scales, because of the time needed to alter biogeochemical cycles and the properties of soil organic matter. Therefore the duration of the monitoring should be prioritized over its frequency if the setup does not allow a good coverage of both.

Integration among disciplines

The very nature of climate change and its impacts is discipline-spanning and therefore requires an integrated approach[25]. Althought the number of interdisciplinary studies related to climate change is increasing steadily[26], there are still many challenges related to interdisciplinary research. These include establishing common terminology, concepts and metrics[25,27,28], a consistently lower funding success for interdisciplinary research projects[29], and a general lack of interdisciplinary research positions[25]. The barriers depend largely on the purpose, forms and extent of knowledge integration, and their combination[30]. Although climate change research developed from multidisciplinarity to interdisciplinarity, and further to transdisciplinarity[31], most collaborative work in environmental research is small-scale rather than large-scale interdisciplinary work[30]. Small-scale integration refers to collaborations between similar partners (for example, different natural science disciplines), while large-scale integration crosses broader boundaries (such as between natural and social science)[30]. Currently, ecosystem services studies are mostly limited to either the natural science aspects or the socio-economic science aspects and rarely cover the entire ecosystem services cascade[32]. This lack of large-scale knowledge integration results in errors along this cascade; both when moving from biodiversity and ecosystem functions to ecosystem services, and when moving from ecosystem services to societal values.

3. Recommendations

Using climate model outputs and technology to refine climate change treatments

A first option to prescribe a projected change in weather dynamics is to alter specific characteristics (such as drought duration, heat wave intensity) in isolation using high-frequency data of ambient weather conditions so that they match future projections. The advantage of this method is that atmospheric conditions can be modified with high-quality field data instead of relying upon less precise regional climate model outputs with lower spatial and temporal resolution. Moreover, if used to manipulate one climate factor at a time, such an approach facilitates a mechanistic understanding of ecosystem responses that can be further extrapolated through modeling. This design may combine two or more factors to provide information about interactions between climate parameters.

Incorporating the complexity of projected changes can also be achieved by using outputs of state-of-the-art climate models. Due to model biases, the appropriate model must be selected very carefully. Global climate models (GCMs) are useful tools for assessing climate variability and change on global to continental scales, typically with a spatial resolution of 100−250 km. To estimate climate variability at more local scales, GCMs are dynamically downscaled using regional climate models (RCMs), which resolve the climate at higher resolutions (typically 10−50 km). The GCM/RCM combinations can then be chosen based on (i) how well models perform against local climate and weather characteristics in the studied ecosystem and (ii) how representative future projections are to the multi-model mean. In this case, one can simulate an ecosystem response to a given climate setup with higher accuracy. However, unlike with a full factorial experiment, it is not possible to attribute an ecosystem response to a given climate factor. Nevertheless, the model-output approach does facilitate the application of increasingly high warming levels by using a global mean temperature gradient (see Section 4). It also addresses the issues of covarying variables, and it can be directly linked with a scenario from the Intergovernmental Panel on Climate Change which would represent a major step towards bridging the gap between climate and ecosystem science.

However, to implement these options it is necessary to control climate conditions and atmospheric composition with high frequency and high accuracy. This can be achieved only with dedicated and advanced equipment. Ecotron infrastructures, which consist of a set of replicated experimental units where environmental conditions are tightly controlled and where multiple ecosystem processes are automatically monitored, are well-suited to fulfill these needs[33]. Such infrastructures have been historically limited to a handful across the world[9], but are becoming increasingly widespread[34–36]. They also offer the opportunity to monitor ecosystem responses at sub-hourly frequencies, making it possible to simultaneously discriminate between short- and long-term ecosystem responses.

Increasing the number and range of climate treatment levels

A gradient design, in which one or several climate factors are applied at increasingly high levels, can substantially increase the resolution of a climate change experiment. This is better suited to quantitatively describing the relationship between a response variable and a continuous climate factor than the more traditional approach of testing ambient versus a single future projection, and allows the collection of quantitative data for ecological models[37]. It also makes it possible to detect nonlinearity, thresholds, and tipping points, and to interpolate and extrapolate ecosystem responses[18]. While such gradient designs should ideally be replicated, unreplicated regression designs can be a statistically powerful way of detecting response patterns to continuous and interacting environmental drivers, provided that the number of levels in the gradient is large enough[37].

To ensure appraisal of the largest possible range of ecosystem responses, the gradient should be as long as possible, even extending beyond the most extreme conditions. Broader treatment modalities can also inform how far a specific ecosystem response is situated relative to its upper or lower tolerance limit. In addition, the levels of the gradient may be spread in a non-linear manner to achieve the highest resolution in the range where the strongest ecosystem responses are expected.

Employing an interdisciplinary approach to better capture responses and interactions

We argue that an overarching objective of climate change experiments is to contribute to the understanding of the impacts that climate change has on nature and society as well as to enlarge our potential for climate adaptation. However, as outlined in Section 2, the lack of large-scale knowledge integration can result in errors along the ecosystem services cascade; first in the step from biodiversity and ecosystem functions to ecosystem services and second from ecosystem services to societal values.

Regarding the first step, thorough quantification of ecosystem services should be based on specific data regarding how the ecosystem is functioning. Many ecosystem service studies use land use as an indicator of ecosystem service delivery[32], but often land use classification cannot capture differences between abiotic conditions and ecological processes that explain differences in service delivery[38]. Therefore, using land use as a simple indicator will result in inappropriate management decisions[38].

Regarding the second step, economists need to be involved early in the process. Although there are many ways in which ecosystem function changes can affect the provision of ecosystem services to society[39]. However, budget constraints necessitate the selection of those ecosystem functions and services that are considered most important to society. A common selection approach is to consider the potential impact of ecosystem changes in terms of human welfare endpoints, often by means of monetary valuation. Ecologists and economists must interact across disciplinary boundaries if ecological experiments are intended to predict these endpoints within an ecosystem services context[40]. Hence, economists need to be involved during the design of ecological experiments in order to ensure that those ecosystem service changes that are most relevant for human welfare are measured and predicted.

We suggest that, the desired large-scale integration can be achieved in several steps, organized in a top-down approach. The first step is to identify the key ecosystem services to value based on welfare endpoints[41]. For most terrestrial ecosystems, this would imply assessing services from the following list: food and raw material production and quality, water supply and quality, C sequestration, depollution, erosion prevention, soil fertility, pest and pathogen control, pollination, maintenance of biodiversity and recreation. The second step consists of identifying the set of variables that best describes the ecosystem functions, processes and structures associated with these services. Based on the literature[42], we suggest the following measures (see also Table 1): (i) vegetation variables (plant community structure, above/belowground biomass, litter quality), (ii) atmospheric parameters (net ecosystem exchange, greenhouse gas emissions), (iii) soil abiotic (pH, texture, electrical conductivity, macro-, micronutrient and pollutant content) and biotic (fauna and microbial community structure, respiration, and biomass) variables, and (iv) all parameters that describe movements of water in the soil-plant-atmosphere continuum (precipitation, leaching, air relative humidity, evapotranspiration, water potential). Air and soil temperatures should also be monitored, since they determine biogeochemical reaction rates. Finally, ecosystem processes, structures and functions need to be translated into services, and ultimately into societal value by expressing them in monetary and non-monetary terms. Measuring all of these variables, integrating them in an ecosystem service framework, and estimating the societal value of these services would require expertise from plant ecologists and ecophysiologists, hydrologists, soil biogeochemists, animal ecologists, microbiologists, pedologists, climatologists, as well as modelers and environmental economists[43].

4. An initial application of the recommendations: The UHasselt Ecotron experiment

Here we describe our proposed interdisciplinary approach in the context of a climate change manipulation using the UHasselt Ecotron experiment.

Ecotron infrastructure

The UHasselt Ecotron facility consists of tightly controlled climate change manipulations of 12 macrocosms (soil-canopy columns of 2 m in diameter and 1.5 m depth), extracted without significant disruption of the soil structure from a dry heathland plot in the 'Hoge Kempen' National Park (50° 59' 02.1" N, 5° 37' 40.0" E) in November 2016. The plot was managed for restoration six years before the sampling. The design of this infrastructure benefited from exchanges through the AnaEE (Analysis and Experimentation on Ecosystems)/ESFRI (European Strategy Forum on Research Infrastructure) project. Some of the infrastructure's features were inspired by the Macrocosms platform of the CNRS Montpellier Ecotron[16]. Each UHasselt Ecotron unit consists of three compartments: the dome, the lysimeter, and the chamber. The dome consists of a shell-shaped dome made of highly PAR (photosynthetically active radiation) transparent material, where wind and precipitation are generated and measured and where the concentration of greenhouse gases (CO_2, N_2O, CH_4), PPFD (photosynthetic photon flux density) and difference between incoming and outgoing short- and long-wave radiation are measured. The lysimeter (equipment for measuring hydrological variations undergone by a body of soil under controlled conditions) contains the soil-canopy column, where soil-related parameters are controlled (including the vertical gradient of soil temperature and water tension) and measured, and is weighed every minute. Suction cups and soil sensors are installed following a triplicated 5 depth design (Fig. S1). The chamber is a gastight room that encloses the lysimeter, where air pressure, air temperature, relative humidity, and CO_2 concentration are controlled and key variables measured in each unit (Fig. S1). The UHasselt Ecotron is linked with a nearby Integrated Carbon Observation System (ICOS) ecosystem tower (https://www.icos-ri.eu/home), which provides real-time data on local weather and soil conditions, with a frequency of at least 30 minutes.

Climate manipulations

A double-gradient approach is adopted: one approach (six units) measures the effect of an altered single factor (here, precipitation regime), while maintaining the natural variation of other abiotic factors, and the other approach (six units) manipulates climate by jointly simulating all covarying parameters, representing increasingly intense climate change. The two approaches are described below. Because they sit isolated in an enclosed facility, it is possible that small initial differences in the soil-canopy core in a given unit will increase with time to the point where it becomes statistically different from the others. Therefore, the units were first distributed within the two gradients using a cluster analysis to minimize the noise in ecosystem responses measured during a test period (see Fig. S2) due to small-scale soil heterogeneity. This clustering was used to distribute the units according to the pattern shown in Fig. 1.

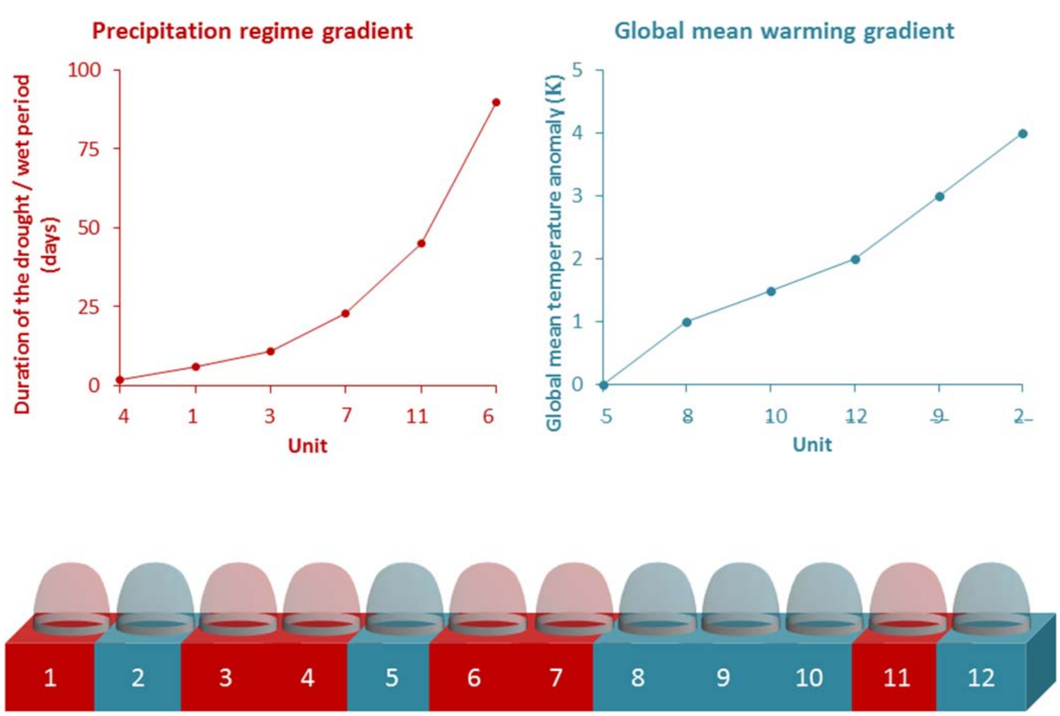

Figure 1. Overview of the two climate change gradient designs in the UHasselt Ecotron experiment. The units have been redistributed to maximize statistical similarity within a gradient prior to the

treatment. Global mean temperature anomalies are computed with respect to the reference period 1951-1955.

Climate change projections for the NW Europe region predict higher probability of both heavier precipitation and longer droughts, without a significant change in yearly precipitation[44]. The precipitation regime gradient uses real-time input from the ecosystem tower nearby, and only alters precipitation events: across the gradient, increasingly long periods (2, 6, 11, 23, 45 and 90 days), based on local climate records from Maastricht, NL[45]) in which precipitation is withheld (dry period) are followed by increasingly long periods in which precipitation is increased (wet period), with the duration of the two periods kept equal within a unit (Fig. 1). Precipitation events during the wet period are increased twofold and are adjusted at the end of the period to avoid altering the yearly precipitation amount.

To drive the second gradient of the UHasselt Ecotron experiment, we use the climate variables produced by an RCM following Representative Concentration Pathway (RCP) 8.5, a high-emission scenario[46]. The gradient itself is determined based on global mean temperature anomalies. In the six units, climates corresponding to a +0 ° to +4 °C warmer world (projected for periods ranging from 1951–1955 to 2080–2089) are simulated (Fig. 1, Fig. S3), by extracting local climate conditions from the RCM for periods consistent with these warming levels (Fig. S3)[47]. This set-up also facilitates comparison of the 'present-day' climate as simulated by the RCM (the +1 °C unit), to the unit driven by ICOS field observations. Moreover, the climate simulated in the +1.5° C unit is reasonably consistent with the lower end of the long-term temperature goals set by the Paris Agreement[48].

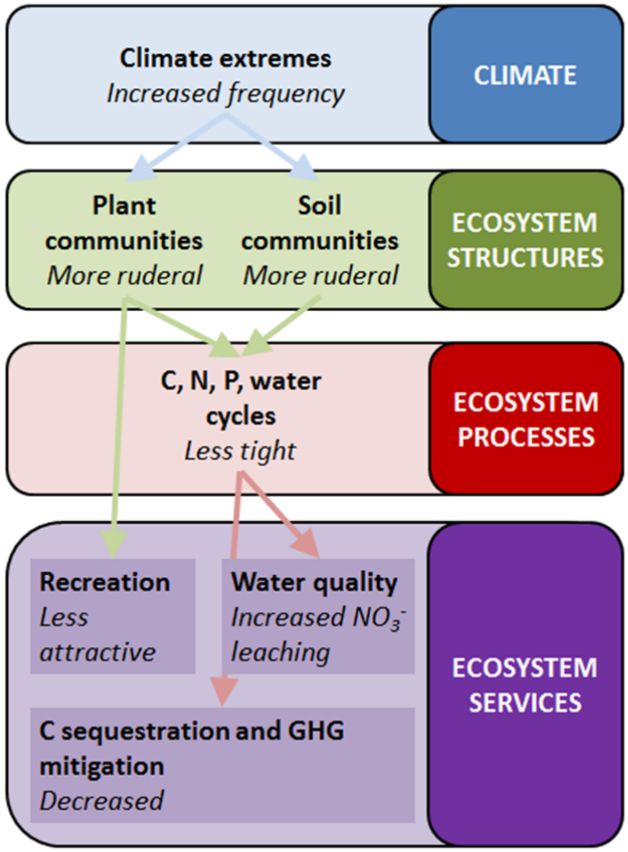

Figure 2. Impact pathway showing the reasoning behind the integration of scientific disciplines in the UHasselt Ecotron experiment. The research hypotheses are given in italics and described in more detail in Fig. S4.

Integrating scientific disciplines for an interdisciplinary ecosystem service approach

As outlined in Section 3, climate change experiments require large-scale knowledge integration to enable more useful estimates of climate change effects on ecosystem functioning and on society. The UHasselt Ecotron facility makes it possible to extend the degree of interdisciplinarity by investigating the entire cascade from climate changes to ecosystem functions, ecosystem services, and, finally, societal values. As such, the ecotron facility contributes to the development towards large-scale knowledge integration on climate change. Consequently, the UHasselt Ecotron experiment brings together several disciplines in an interdisciplinary framework (Fig 2). With input from other involved disciplines, climatologists design the protocols for climate manipulations and plant ecologists monitor plant communities in each ecotron unit. Numerical models for water movement within one unit are developed by mathematicians and hydrologists. Ecotron output on C cycling is fed into a soil C model[49], both for calibration and prediction purposes. Community modelers improve the power of this model by accounting for the soil community structure and species interactions (food web). The specific role of soil organisms in soil biogeochemistry is investigated by microbial and soil fauna ecologists. This is inferred from variation in responses of different functional groups such as nitrogen fixers, mycorrhizal fungi and different feeding guilds of soil fauna, combined with additional separate experiments, both in the field and *in vitro*. The outputs of the measurements above (see Table 1) allow experts in ecosystem ecology to quantify ecosystem services. Environmental economists express the change in ecosystem services provided using best-practice monetization approaches[50]. For example, water quality regulation is assessed as the prevented cost of intensified water treatment or use of other water resources. Measurements of vegetation, soil abiotic parameters and the water balance make it possible to quantify this benefit. Carbon sequestration is assessed as the prevented cost from increased global temperature, which can be quantified based on vegetation, air parameters and soil abiotic parameters measurements. Maintenance of biodiversity and recreation can be assessed based on measurements of vegetation.

We note that (monetary) estimates from an individual study can often not be applied directly for generating policy-recommendations[51], especially for complex and spatially heterogeneous problems such as climate change impacts on ecosystems. However, meta-analyses need to rely on data generated by primary studies that estimate the societal cost (or benefit) of changes in specific services provided by a specific ecosystem at specific location(s). In this regard, the UHasselt Ecotron experiment can also provide valuable input data for dedicated policy-guiding analyses[52].

Table 1. Measured variables in the UHasselt Ecotron experiment and links with ecosystem functions, services, and values. Left-hand side of the table: ecosystem services. Right-hand side: variables measured in the ecotron experiment. Lower part of the table: illustration of how the societal value of four of the ecosystems services will be assessed.

ECOSYSTEM SERVICES: Food	Raw materials	**Water quality**	**C sequestration**	Erosion prevention	**Maintenance of biodiversity**	**Recreation**	Climate regulation	Water retention	Soil fertility	Depollution	Pathogen control	MEASURED VARIABLES: **Variable category**	**Variable**	**Frequency of measurement**
o	o	o	o	o	o	o						Vegetation	Plant community structure	6 months
o	o	o	o	o	o								Shoot & root biomass	6 months
			o									Air parameters	Net ecosystem exchange (NEE)	30 min
							o						Temperature	2 min
			o										GHG emissions (CH4, N2O)	2 min
				o				o	o			Soil abiotic parameters	Texture	1 year
							o	o					Temperature	2 min
			o						o				Biochemical composition	1 year
		o						o					Electrical conductivity	30 min
		o						o					Soil pore water chemistry	2 weeks
										o			Available pollutant concentration	1 year
									o		o	Soil biotic parameters	Fauna community structure	6 months
				o					o		o		Microbial community structure	6 months
									o				Mineralization rate	1 year
		o		o				o				Water balance	Precipitation	30 min
		o						o	o	o			Leaching	30 min
		o						o					Relative humidity	30 min
		o						o					Evapotranspiration	30 min
		o						o					Soil water potential	30 min

Ecosystem service	ECONOMIC VALUATION
Water quality	Prevented cost of intensified water treatment or use of other water resources
C sequestration	Prevented damage cost from increased global temperature
Maintenance of biodiversity	Non-use value of continued existence of biodiversity
Recreation	Use value of recreational enjoyment

5. The place of the suggested design within the landscape of climate change experiments

A comprehensive understanding of ecosystem responses to climate change can only be achieved through the use of a broad range of different, complementary experimental designs, all of which can be integrated through modeling. The experimental design suggested here exhibits a unique set of advantages and drawbacks, which makes it suited to tackle specific needs within the climate change experiments landscape.

Strengths and limitations of the design

The strengths of the suggested design comprises (1) high-performance microclimate conditioning, both above- and belowground, which makes it possible to approximate field conditions while maintaining control, (2) high-frequency automated measurements of ecosystem functions and thus of treatment impact thereon, and (3) a large-scale interdisciplinary approach. The first two strengths are inherent to the ecotron research infrastructure, while the large-scale integration can theoretically be implemented in any climate change experiment. However, we consider ecotron infrastructures to be particularly suitable for such an interdisciplinary approach, because of the high-end climate control and the broad range of functions monitored at a high frequency.

With respect to (1), studies focusing on ecosystem functions, processes and structures that are highly sensitive to soil temperature and soil water potential would benefit most from being conducted in ecotrons (for example, soil CO_2 exchange and C sequestration, growth and activity of soil microbes and soil fauna), as the lysimeter component can generate very precise lower boundary conditions and thus realistic vertical soil profiles of temperature and soil water status. With respect to (2), studies in which the high-resolution temporal pattern of ecosystem functions and their coupling is important would also benefit from ecotron infrastructures, as it is difficult to measure these parameters manually across long time scales. For example, simultaneous automated measurement of the carbon, water and mineral nutrient cycles makes it possible to disentangle their interactions in a range of climate conditions, and to feed control mechanisms into models.

A first set of constraints in the usefulness of the experimental design described in this paper stems from the scale limitation of the experimental units. Ecotrons can accommodate plants only of small stature (less than two meters in height), which excludes forests and tall crops. For the same reason, the impact of megafauna such as grazers or top predators cannot be tested. Results obtained in macrocosms only integrate small-scale (less than one meter) variability, which leads to a lack of accuracy when scaling up to ecosystem.

Second, it may be difficult to financially support this type of experiment on the time scale of ecosystem responses (10 years or more)[53]. Ecosystem shifts to alternative stable states may remain undetected if the funding period is shorter than the period required for the ecosystem to shift. A partial solution for this would be to adopt a gradient design with increasingly late endpoints of projected climate change; this would allow for some extrapolation of ecosystem response in time (trajectories), which is possibly enough to estimate ranges of this response in the longer term.

Third, macrocosms in ecotron facilities are isolated from their ecosystem of origin. Hence genetic input from propagules or pollination probably differ significantly from the field, which can be an issue, especially in long-term experiments. This could be mitigated in two ways. The first is by minimizing sampling disturbance, by sampling for soil microbes and soil fauna not more than twice a year, using 10 cm diameter soil cores, this would account for only 1.5% of total soil surface annually. The second way is by replacing soil sampling cores in the lysimeter by cores taken from the same ecosystem. This would also avoid holes at the soil surface that may alter water flow through the soil column. Furthermore, field traps to collect airborne propagules can be collected yearly and their content spread on the enclosed surface of the soil-canopy columns. These solutions would at least ensure fresh genetic input into the system, even though this input may be different in the field in future conditions.

Finally, radiation in ecotron enclosures sometimes differ than in the field. Artificial LED-lightning allows to control radiation precisely but is yet not able to reach the same radiation level as in the field, while ambient lightning can disrupt its synchronization with temperature or precipitation. This may be an issue while simulating heatwaves and droughts, which have more sunshine hours than wet periods [54].

Complementarity with other climate change experiments

The weaknesses of the proposed design (small spatial scale, potentially insufficient time-scale, lack of interaction with the surrounding environment) can be mitigated further through the use of complementary experiments, which might even be partially integrated into the overarching approach. For example, owing to small spatial scale, the results might have limited validity as a predictor of ecosystem responses at other sites and in other habitats. Running experiments in parallel across multiple climates and locations with the same methodology, also known as "coordinated distributed experiments" (CDEs), would be better suited for this purpose as it allows extrapolation and generalization of results while correcting for effect size[55]. For example, such a design makes it possible to study plant response to nutrient addition and herbivore exclusion[56]; and ecological responses to global change factors across 20 eco-climate domains using a set of observatory sites[57]. In fact, a coordinated distributed experiment using the design presented in Section 4, and testing the same climate gradient in different ecosystems across several ecotron facilities would combine the high generalization potential of CDEs with the precision of ecotrons.

A second area for potential complementarity and integration is translocation experiments. These experiments are well suited for long-term observations due to their relatively low funding requirements and relative ease of implementation, and the soil macrocosms used in these experiments are still connected to their surrounding environment[17]. However, the functioning of the ecosystem is monitored less comprehensively and frequently within these types of experiments and the influence of different climate factors on ecosystem functioning cannot be disentangled. Consequently, running an ecotron and a translocation experiment in parallel on the same ecosystem with similar climate treatments would make it possible to estimate the effect size of the connection with the surrounding environment on ecosystem response to climate change. This information can then, in turn, be used to correct the outputs of future ecotron experiments by accounting for the isolation factor.

Usefulness of the suggested design for modeling ecosystem response to climate change

While ecosystem models can be evaluated and calibrated using a range of data sources, including sites in different climate zones and long-term experiments without climate manipulation[58], data from well-controlled, replicated and highly instrumented facilities such as those described here are invaluable for testing the process understanding encapsulated in the models, and for testing model behavior against detailed, multi-parameter observations[36]. Models that are tested and, where necessary, calibrated against such data can then be evaluated against data from other sites. If the outputs do not prove to be generalizable, the information derived from testing the model could be used to refine the experimental design and explain variation in the measured values. If the outputs prove generalizable, the models can be used across larger temporal and spatial scales to project potential impacts of future climate change[59,60].

6. Conclusion

The effects of climate change on ecosystem functioning have far-reaching consequences for society. Here we present a type of experiment that is designed to estimate the amplitude and dynamics of ecosystem responses to climate change, and the consequences for ecosystem services. We have outlined that climate change experiments are facing three types of challenges: limitations in addressing the complexity of climate change in terms of control of environmental variables, constraints in the number and range of climate level treatments, and restrictions in scope. We have suggested ways to address these challenges: improving computational and technological capabilities, increasing the number and range of climate treatment levels, and employing an interdisciplinary approach. We illustrated these suggestions through a case study where they have been implemented, and outlined the place of this design in the broader landscape of climate change experiments.

We foresee that the holistic approach outlined in this perspective could yield more reliable, quantitative predictions of terrestrial ecosystem response to climate change, and could improve knowledge on the value of ecosystem services and their links with ecosystem processes. We expect these results to be of interest for society beyond just scientists: they provide nature managers with predictions on ecosystem responses to help them decide on ecosystem management practices in the mid- and long-term, and that they will explain to policymakers and the wider public the societal impact of ecosystem changes induced by climate change at a more detailed, ecosystem-specific level.

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Authors' contributions

FR and RM took the lead in writing the manuscript and received input from all co-authors. The initial conceptualization of this manuscript was discussed during a consortium meeting. All authors proofread and provided their input to different draft versions and gave their final approval for submission.

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